
CEROPEGIA (APOCYNACEAE, CEROPEGIEAE, STAPELIINAE): PARAPHYLETIC BUT STILL TAXONOMICALLY SOUND¹

Ulrich Meve² and Sigrid Liede-Schumann²

ABSTRACT

Even though the species-rich genus *Ceropegia* L. (Apocynaceae, Ceropegieae) is convincingly characterized by its pitfall flowers, investigation of non-coding markers of chloroplast DNA (cpDNA) (*trnT-L* and *trnL-F* spacers and the *trnL* intron) and nuclear ribosomal DNA (nrDNA) (ITS) has shown that *Ceropegia* is twice paraphyletic. The 36 analyzed *Ceropegia* taxa scatter over a grade of seven clades. One clade is shared by *Ceropegia* and all *Brachystelma* R. Br. species investigated, making *Ceropegia* (without *Brachystelma*) paraphyletic. All endemic Madagascan *Ceropegia* taxa investigated and the East African *C. robynsiana* Werderm. share a terminal, but not further-resolved clade with the stapeliads. Thus, again, *Ceropegia* without the stapeliads is paraphyletic. These results are incongruent with current taxonomy. In the absence of adequate morphological, anatomical, or karyological characters supporting a taxonomic reclassification of the genus in accordance with the retrieved clades of the phylogenetic analysis, it is proposed that the current taxonomy be maintained.

Key words: *Brachystelma*, *Ceropegia*, ITS, molecular systematics, morphology, paraphyly, phylogeny, *trnL* intron, *trnT-L* and *trnL-F* spacers.

With more than 180 species, *Ceropegia* L. (Apocynaceae, Asclepiadoideae) represents the largest genus in the Old World tribe Ceropegieae, where it belongs to the subtribe Stapeliinae G. Don together with *Brachystelma* R. Br. and the 40 stapeliad genera, which form a statistically strongly supported clade (100% bootstrap percentage [BP]) in previous cladistic analyses of chloroplast DNA (cpDNA) and nuclear ribosomal DNA (nrDNA) sequence data (cf. Meve & Liede, 2002a, 2004). The distribution of *Ceropegia* extends across the tribal range from West Africa to Australia, with two main centers of distribution: East Africa including southeastern Africa (115 species) and India (40 species). Additional subcenters are found in Madagascar (20 species) and China (17 species). The fascinating forms and function of the *Ceropegia* lantern and pitfall flowers have long attracted the attention of biologists dealing with aspects of both flower morphology and pollination biology (e.g., Vogel, 1961, 1962), as well as horticulturists, because *C. linearis* E. Mey. subsp. *woodii* (Schltr.) H. Huber is an important ornamental. Also, the extreme variability of flower morphology in the genus and within many specific and infraspecific taxa has been well utilized by taxonomists. Over 500 different taxon names have been described, of which an increasing number have been sunk into synonymy

(Meve & Mangelsdorff, 2001; Meve et al., 2001; Meve, 2002). The current concept of relatively few but variable species is increasingly supported by molecular data demonstrating low genetic divergence, even between morphologically rather different-looking variants, as in the *C. aristolochioides* complex (Meve et al., 2001). In this random amplified polymorphic DNA (RAPD) analysis, estimates of genetic distances were low (0.150) to very low (0.008). Apart from regional taxonomic treatments (Dyer, 1983; Ansari, 1984; Meve & Liede, 1994a; Masinde, 2000; Gilbert, 2003), only one full revision of *Ceropegia* (151 species; Huber, 1957) and an almost complete treatment (160 species, omitting only the ca. 25 non-succulent species; Meve, 2002) are available. Infrageneric classifications were proposed by both Schumann (1895) and Huber (1957). Schumann (1895) created three sections on the basis of the degree of corolla fusion and orientation of the lobes. Huber (1957) discarded Schumann's (1895) concept, assigning species to 20 sections (and 23 series). Meve and Liede (1994a) additionally described another section, *Ceropegia* sect. *Dimorpha* Huber ex Meve & Liede, for the stem-succulent taxa endemic to Madagascar. Huber (1957) treated *Riocreuxia* Decne. as a section of *Ceropegia*, but Dyer (1980) correctly reinstated the genus, as demonstrated morphologically

The skill and meticulous laboratory work of Angelika Täuber, Bayreuth, is gratefully acknowledged. We thank the many colleagues and collectors who contributed plant material; Ernst Specks, Hückelhoven, also provided photos of *Ceropegia* from Tanzanian habitats. Mary Endress (Zürich, Switzerland) and Victoria Hollowell (St. Louis, Missouri) kindly contributed much to the improvement of the manuscript.

²Department of Plant Systematics, University of Bayreuth, 95448 Bayreuth, Germany. ulrich.meve@uni-bayreuth.de.

(Meve, 1998) and later molecularly (Meve & Liede, 2002a, 2004). The pitfall flowers of *Riocreuxia* are now regarded as a case of homoiology (parallel evolution; Meve & Liede, 1999, 2004). As criticized by Dyer (1980) and Meve and Liede (1994a), Huber's subdivision of the genus, which is based nearly exclusively on flower morphological characters, is highly artificial. To date, no phylogenetic analysis of the genus *Ceropegia* as a whole is available. Considering the increased awareness of the extreme variability and the many parallelisms, both vegetative and floral, in *Ceropegia* (and Ceropegieae), an analysis of the infrageneric phylogeny of *Ceropegia* is overdue. In the present paper we focus on four main goals: (1) reconstruction of the phylogeny of *Ceropegia* using cpDNA and nrDNA sequence data and comparison with root and flower morphology; (2) deduction of the geographic origin of *Ceropegia* and its colonization of Madagascar; (3) reconsideration of the status of *Brachystelma*; and (4) discussion on how to translate our phylogeny into a reasonable taxonomy and how to deal with paraphyletic taxa (cf. Brummitt, 1996, 2002; Grant, 2003).

MATERIAL AND METHODS

TAXA SAMPLED

The material used in this study is summarized in Table 1, including 69 voucher specimens, authors of species, and donors or collectors of material. For the ingroup, 36 species of *Ceropegia* and 10 species of *Brachystelma* were chosen, covering the range of diversity and distribution of the genus. As outgroups, representatives were chosen from two other subtribes of Ceropegieae (cf. Meve & Liede, 2004), Anisotominae (*Anisotoma* Fenzl., *Neoschumannia* Schltr., *Riocreuxia*, and *Sisyranthus* E. Mey.) and Leptadeniinae (*Leptadenia* R. Br. and *Orphanthera* Wight), and from the most distant outgroup, Marsdenieae (*Gymnema sylvestre* (Retz.) Schult.; Table 1). Representatives of eight species of different stapeliad genera were selected as the closest outgroup.

CHROMOSOME NUMBERS AND CHROMOSOME LENGTH

Chromosome numbers and chromosome sizes were established from adventitious root tip squash preparations. Ten mitotic metaphase plates of each sample were investigated. The root tips were pretreated in 0.002 M hydroxyquinoline for 4 hr. at 20°C (Tjio & Levan, 1950), fixed in Carnoy's solution for 24 hr. at 20°C, and stained in carmine for 24 hr. at 60°C (Snow, 1963). For cytological investigation, a Leitz Orthoplan microscope (Leica Microscopic Systems,

Wetzlar, Germany) was used. The total length of all chromosomes in the genome was measured on maximally contracted chromosomes on the basis of camera lucida pencil drawings.

DNA EXTRACTION AND PCR

DNA was isolated from fresh leaf and stem tip tissue according to Doyle and Doyle (1987). Polymerase chain reaction (PCR) primers and protocol for the plastid *trnT-L* and *trnL-F* spacers and the *trnL* intron correspond to Taberlet et al. (1991). Sequences were obtained on an ABI Prism Model 310 Version 3.0 sequencer (Applied Biosystems, Foster City, California). One hundred seventeen cpDNA sequences and 32 ITS sequences were used from previous studies of the authors (cf. Meve & Liede, 2001, 2004), and 99 cpDNA and 33 ITS sequences were newly obtained for this study (Table 1). No ITS sequences could be generated for *Brachystelma franksiae* N. E. Br., *B. schizoglossoides* N. E. Br., and *Ceropegia maccannii* Ansari. The ITS sequence of the marsdeniad *Gymnema sylvestre* could not be aligned with the ITS sequences of the Ceropegieae taxa and was therefore omitted. All sequences have been deposited at the European Molecular Biology Laboratory (EMBL) Nucleotide Sequence Database (for EMBL accession numbers, see Table 1).

DNA DATA ANALYSIS

Sequences were pre-aligned with Sequence Navigator Version 1.0.1 (Perkin-Elmer, Inc., Waltham, Massachusetts); the alignment was cleaned manually. Indels were coded as missing throughout. Phylogenetic analysis and tests for clade support were performed using PAUP version 4.0b10 (PPC) (Swofford, 1998). Phylogenies were generated using Fitch parsimony as implemented in PAUP* employing heuristic searches, with 1000 replicates, random stepwise addition, MULPARS off, and tree bisection-reconnection (TBR) branch swapping. The resulting trees were then used as starting trees for a second round of searches with MULPARS on. Our search strategy was aimed at finding as many different islands of trees as possible. Sets of equally parsimonious trees recovered from each analysis were summarized by strict consensus. BPs (Felsenstein, 1985) derived from 1000 replicates (saving a maximum of 100 trees per replicate) were calculated as measures of support for individual clades. To test whether cpDNA data and ITS data can be combined, a partition homogeneity test, as implemented in PAUP*, was conducted.

Table 1. Voucher and locality information and EMBL accession numbers for plant material used in the molecular studies (newly published sequences are marked by *).

Species	Origin	Voucher	EMBL acc. no. <i>trnT-L</i> spacer <i>trnL</i> intron <i>trnL-F</i> spacer	EMBL acc. no. ITS
Outgroup				
<i>Gymnema sylvestre</i> (Retz.) Schult. (Marsdenieae)	Cameroon: E Mokolo	<i>Mere</i> 919 (B, UBT)	AJ402118 AJ402137 AJ402142	—
<i>Anisotoma cordifolia</i> Fenzl	South Africa: Eastern Cape	<i>Nicholas</i> 2811 (UDW)	AJ410016 AJ410017 AJ410018	AJ310780
<i>Apteranthes europaea</i> (Guss.) Plowes var. <i>europaea</i>	Spain: Capo da Gata	<i>Albers</i> 87-23-004-20 (MSUN)	AJ488312 AJ488313 AJ488314	AJ488773
<i>Boucerosia frerei</i> (G. D. Rowley) Meve & Liede	India: Maharashtra	<i>Sakaria</i> sub <i>K</i> 781 (MSUN)	AJ488324 AJ488325 AJ488326	AJ488777
<i>Caralluma arachnoidea</i> (P. R. O. Bally) M. G. Gilbert	Kenya: Rukanga	<i>Mere</i> 934 (UBT)	AJ410037 AJ410038 AJ410039	AJ310785
<i>Caudanthera edulis</i> (Edgew.) Meve & Liede	Oman: W Salalah	<i>Butler</i> C312 (UBT)	AJ402116 AJ402139 AJ402140	AJ402162
<i>Desmidorchis flava</i> (N. E. Br.) Meve & Liede	Oman: Mugsail	<i>Collenette</i> s.n. (MSUN)	AJ488357 AJ488358 AJ488359	AJ488789
<i>Echidnopsis repens</i> R. A. Dyer & Verdoorn	Kenya: Mt. Maktau	<i>Mere</i> 942 (MSUN, UBT)	AJ488381 AJ488382 AJ488383	AJ488797
<i>Hoodia officinalis</i> (N. E. Br.) Plowes	Namibia: E Aus	<i>Mere</i> 176 (UBT)	AJ488393 AJ488394 AJ488395	AJ488801
<i>Larryleachia cactiformis</i> (Hook.) Plowes	South Africa: Numees	<i>Teissier</i> 097 (UBT)	AJ402120 AJ402135 AJ402144	AJ402159
<i>Leptadenia arborea</i> (Forssk.) Schweinf.	Egypt: Asswan	<i>Heneidak</i> s.n. (Suez Canal Univ. Herb.)	AJ574832 AJ574833 AJ574834	AM493305*
<i>Leptadenia hastata</i> Decne.	Gambia: Abouko NP	<i>S. Huber</i> s.n. (UBT)	AJ410055 AJ410056 AJ410057	AJ310787
<i>Neoschumannia cardinea</i> (S. Moore) Meve	Tanzania: Amani Forest Reserve	<i>Liede & Mere</i> 3359 (B, UBT)	AJ410049 AJ410050 AJ410051	AJ310790
<i>Neoschumannia kamerunensis</i> Schltr.	Cameroon: Mt. Cameroon	<i>Mere & Etuge</i> 910 (B, K, UBT)	AJ410052 AJ410053 AJ410054	AJ310791
<i>Orthanthera albida</i> Schinz	Namibia: W Marinkas Quellen	<i>Bruyns</i> 7262 (BOL)	AJ410058 AJ410059 AJ410060	AJ310792
<i>Orthanthera jasminiflora</i> (Decne.) N. E. Br. ex Schinz	Botswana: Shakawe	<i>Bruyns</i> 6491 (BOL, K)	AJ410064 AJ410065 AJ410066	AJ310794
<i>Quaqua incarnata</i> (L. f.) Bruyns subsp. <i>incarnata</i>	South Africa: S Klawer	<i>Albers & Mere</i> 06 (MSUN)	AJ488453 AJ488454 AJ488455	AJ488821

Table 1. Continued.

Species	Origin	Voucher	EMBL acc. no. <i>trnT-L</i> spacer <i>trnL</i> intron <i>trnL-F</i> spacer	EMBL acc. no. ITS
<i>Riocreuxia burchellii</i> K. Schum.	South Africa: KwaZulu-Natal	<i>ex hort. Shirley</i> (MSUN)	AJ488306 AJ488307 AJ488308	AJ488771
<i>Riocreuxia torulosa</i> Decne.	South Africa: KwaZulu-Natal	<i>Edwards s.n.</i> (UDW)	AJ574841 AJ574842 AJ574843	AM493295*
<i>Sisyranthus compactus</i> N. E. Br.	South Africa: Kei Mouth	<i>Nicholas 2825</i> (UDW)	AJ410067 AJ410068 AJ410069	AJ310795
<i>Sisyranthus trichostomus</i> K. Schum.	South Africa: KwaZulu-Natal	<i>Ollerton 245</i> (NU)	AJ574846 AJ574845 AJ574844	AM493296*
<i>Sisyranthus virgatus</i> E. Mey.	South Africa: KwaZulu-Natal	<i>Nicholas & Hariparsaad</i> 2855 (UDW)	AJ574847 AJ574848 AJ574849	AM493297*
<i>Stapelia glanduliflora</i> Mass.	South Africa: S Klawer	<i>Albers & Meve 04</i> (MSUN)	AJ402127 AJ402128 AJ402151	AJ402152
Ingroup				
<i>Brachystelma burchellii</i> (Decne.) Peckover	South Africa: Bloemfontein	<i>Peckover sub Specks</i> 3156 (UBT)	AJ410046 AJ410047 AJ410048	AJ310789
<i>Brachystelma christianeae</i> Peckover	South Africa: Nkandla	<i>Peckover sub Specks</i> 2540 (UBT)	AJ410070 AJ410071 AJ410072	AJ310796
<i>Brachystelma ellipticum</i> A. Rich. (= <i>B. lineare</i> A. Rich.)	Ethiopia: Bahir Dar	<i>Specks 432</i> (K, MSUN)	AJ410019 AJ410020 AJ410021	AJ310781
<i>Brachystelma filifolium</i> (Schltr.) Peckover	South Africa: White River	<i>Peckover sub Specks</i> 2540 (UBT)	AJ410073 AJ410074 AJ410075	AJ310797
<i>Brachystelma frankisiae</i> N. E. Br.	South Africa: KwaZulu-Natal	<i>Nicholas 2846</i> (UDW)	AJ410022 AJ410023 AJ410024	—
<i>Brachystelma macropetalum</i> (Schltr.) N. E. Br.	South Africa	<i>Peckover sub Specks</i> 2986 (MSUN)	AJ410025 AJ410026 AJ410027	AJ310782
<i>Brachystelma nanum</i> (Schltr.) N.E. Br.	South Africa	<i>Peckover sub Specks</i> 2988 (UBT)	AJ410028 AJ410029 AJ410030	AJ310783
<i>Brachystelma pygmaeum</i> N. E. Br. subsp. <i>flavidum</i> (Schltr.) R. A. Dyer	South Africa: KwaZulu-Natal	<i>Ward s.n.</i> (UDW)	AJ410031 AJ410032 AJ410033	AJ310784
<i>Brachystelma rubellum</i> (E. Mey.) Peckover	Tanzania: Arusha Distr., Lake Chala	<i>A. & C. Hemp 2665</i> (UBT)	AJ410076 AJ410077 AJ410078	AJ310798
<i>Brachystelma schizoglossoides</i> (Schltr.) N. E. Br.	South Africa: Eastern Cape	<i>Nicholas 2815</i> (UDW)	AJ410034 AJ410035 AJ410036	—
<i>Ceropegia abyssinica</i> Decne.	Tanzania: Singida	<i>Specks 1052</i> (UBT)	AM491523* AM491524* AM491525*	AM493298*

Table 1. Continued.

Species	Origin	Voucher	EMBL acc. no. <i>trnT-L</i> spacer <i>trnL</i> intron <i>trnL-F</i> spacer	EMBL acc. no. ITS
<i>Ceropegia albisepta</i> Jum. & H. Perrier	Madagascar: Toliara	<i>Teissier</i> 24 (UBT)	AM491526* AM491527* AM491528*	AM493299*
<i>Ceropegia ambovombensis</i> Rauh & Gerold	Madagascar: Ambovombe	<i>Rauh</i> 74872 (HEID)	AM491531* AM491530* AM491529*	AM493300*
<i>Ceropegia arabica</i> H. Huber	Yemen	<i>IPPS</i> 2852 (UBT)	AM491532* AM491533* AM491534*	AM493301*
<i>Ceropegia aristolochioides</i> Decne. subsp. <i>deflersiana</i> Bruyns	Yemen: N Taizz, Al-Qaidah	<i>Řičánek & Hanáček</i> 246 (UBT)	AM491535* AM491536* AM491537*	AM493302*
<i>Ceropegia bulbosa</i> Roxb.	India: s. loc.	<i>Rowland (Butler</i> <i>C</i> 726) (UBT)	AJ488342 AJ488343 AJ488344	AJ488783
<i>Ceropegia crassifolia</i> Schltr.	South Africa: KwaZulu-Natal	ex hort. sub <i>Specks</i> 191 (UBT)	AM491538* AM491539* AM491540*	AM493303*
<i>Ceropegia cufodontii</i> Chiov.	Ethiopia: Shewa Region, W Ambo	<i>Liede & Mere</i> 3522 (UBT)	AM491541* AM491542* AM491543*	AM493304*
<i>Ceropegia cumingiana</i> Decne.	Philippines: Luzon, Mt. Makiling	<i>Liede</i> 3250 (ULM, UBT)	AM491544* AM491545* AM491546*	AM493294*
<i>Ceropegia denticulata</i> K. Schum. ex Engl.	Kenya: Mt. Kasigau	<i>Masinde & Mere</i> 870 (MSUN)	AM488349* AM488348* AM488347*	AM493291*
<i>Ceropegia dichotoma</i> Haw.	Spain: Canary Islands, Tenerife	<i>Mere</i> s.n. (MSUN)	AM488350* AM488351* AM488352*	AM493290*
<i>Ceropegia distincta</i> N. E. Br.	Tanzania: Amani	<i>Liede & Mere</i> 3376 (UBT)	AJ488345* AJ488346* AJ488347*	AJ488784
<i>Ceropegia filiformis</i> (Burch.) Schltr.	South Africa: Northern Cape	<i>Bruyns</i> 6683 (MSUN)	AM488355* AM488354* AM488353*	AM493289*
<i>Ceropegia foliosa</i> Bruyns	Yemen: N Yemen, W Gum'a	<i>Mangelsdorff</i> Y23 (UBT)	AM488356* AM488357* AM488358*	AM493288*
<i>Ceropegia gilgiana</i> Werderm.	Tanzania: Singida, SW Itigi	<i>E. & M. Specks</i> 1039 (UBT)	AM488361* AM488360* AM488359*	AM493287*
<i>Ceropegia humbertii</i> H. Huber	Madagascar: Antsiranana	<i>Mangelsdorff</i> M22 (MSUN)	AM488362* AM488363* AM488364*	AM493286*
<i>Ceropegia intermedia</i> Wight	India: Tamil Nadu, Ebanad	<i>Bruyns</i> 5903 (UBT)	AM488367* AM488366* AM488365*	AM493285*
<i>Ceropegia juncea</i> Roxb.	India: Tamil Nadu, S Nagercoil	<i>Řičánek & Hanáček</i> 92 (UBT)	AJ428798 AJ428799 AJ428800	AJ488785
<i>Ceropegia konasita</i> Masinde	Kenya: Taita, Bura	<i>Masinde & Mere</i> 854 (EA)	AM488368* AM488369* AM488370*	AM493284*

Table 1. Continued.

Species	Origin	Voucher	EMBL acc. no. <i>trnT-L</i> spacer <i>trnL</i> intron <i>trnL-F</i> spacer	EMBL acc. no. ITS
<i>Ceropegia linearis</i> E. Mey. subsp. <i>woodii</i> (Schltr.) H. Huber	ex hort.	<i>Meve s.n.</i> (UBT)	AM488374* AM488375* AM488376*	AM493292*
<i>Ceropegia longifolia</i> Wall.	Bhutan: Wangduephodrang	<i>Liede 3280</i> (UBT)	AM488371* AM488372* AM488373*	AM493283*
<i>Ceropegia maccannii</i> Ansari	India: Maharashtra	<i>Řičánek s.n.</i> (UBT)	AM488379* AM488378* AM488377*	—
<i>Ceropegia meleagris</i> H. Huber	Nepal: s. loc.	<i>ex Shirley s.n.</i> (MSUN)	AM488380* AM488381* AM488382*	AM493282*
<i>Ceropegia meyeri-johannis</i> Engl.	Kenya: Mt. Kasigau	<i>Meve 936</i> (K, MSUN)	AM488385* AM488384* AM488383*	AM493281*
<i>Ceropegia monticola</i> W. W. Sm.	China: Yunnan, Lunan Distr.	<i>Schneidt & Frazer</i> <i>96-145</i> (UBT)	AM491586* AM490376* AM490377*	AM493306*
<i>Ceropegia nilotica</i> Kotschy	Kenya: Voi Distr., Mbololo	<i>Masinde 836</i> (EA)	AJ402117* AJ402138* AJ402141*	AJ402161
<i>Ceropegia pubescens</i> Wall.	Nepal: Anapurna, Komrong Hill	<i>Gerl 637</i> (UBT)	AM490380* AM490379* AM490378*	AM493280*
<i>Ceropegia racemosa</i> N. E. Br.	Tanzania: Arusha Distr., Lake Chala	<i>Liede & Meve 3355</i> (UBT)	AM490381* AM490382* AM490383*	AM493279*
<i>Ceropegia robynsiana</i> Werderm.	Kenya: s. loc.	<i>Pierce 1244</i> (EA)	AM490386* AM490385* AM490384*	AM493278*
<i>Ceropegia rupicola</i> Deflers	Yemen: S Manákhah	<i>Mangelsdorff Y13</i> (UBT)	AM490387* AM490388* AM490389*	AM493277*
<i>Ceropegia sankuruensis</i> Schltr.	Cameroon: Mt. Cameroon	<i>Meve 908</i> (MSUN)	AM490392* AM490391* AM490390*	AM493276*
<i>Ceropegia saxatilis</i> Jum. & H. Perrier	Madagascar: Antsiranana	<i>Mangelsdorff M21</i> (MSUN)	AJ410040* AJ410041* AJ410042*	AJ310786
<i>Ceropegia simoneae</i> Rauh	Madagascar: Toliara, Tsihombé	<i>Rauh 73113</i> (HEID)	AM490393* AM490394* AM490395*	AM493275*
<i>Ceropegia striata</i> Meve & Masinde	Madagascar: Antsirabe	<i>Rauh 75007</i> (HEID)	AJ410043 AJ410044 AJ410045	AJ310788
<i>Ceropegia variegata</i> Decne.	Kenya: N Maralal	<i>Masinde & Meve 871</i> (MSUN)	AM490398* AM490397* AM490396*	AM493274*
<i>Ceropegia yemenensis</i> Meve & Mangelsdorff	Yemen: Ussab al Ali Massiv	<i>Mangelsdorff Y24</i> (B. FR, UBT)	AM490399* AM490400* AM490401*	AM493293*

RESULTS

WHAT CHARACTERIZES *CEROPEGIA*?

Flower morphology. Reinvestigating the morphology of all taxa analyzed molecularly and studying the generic circumscriptions presented for *Ceropegia* (Huber, 1957; Dyer, 1983; Bruyns, 1985; Meve, 2002), it becomes apparent that *Ceropegia* species possess the following significant characters/character states (Figs. 1A, 2): (1) inflorescences with at least a short peduncle (reduced only in a few highly derived taxa) and short, erect pedicels consisting of soft, watery, and non-lignified tissue; (2) corolla tubes longer than the lobes, basally inflated, apically tapering, inside with more or less stiff hairs (rarely absent, then tube inside slippery smooth); (3) corolla lobes mostly apically fused, leaving five small openings in the sinuses; (4) gynostegia and corona as in subtribe Stapeliinae (e.g., *Brachystelma*, *Caralluma* R. Br. s. str.; cf. Meve, 1998) but with staminal corona lobes fairly long and overtopping the anthers (Figs. 2B, E; except for *Ceropegia crassifolia* Schltr. p.p. and *C. dorjei* C. E. C. Fisch.); and (5) micromyiophilous pollination. The highly specialized and complex pitfalls trap small flies predominantly of the families Ceratopogonidae, Chloropidae, Milichidae, and Phoridae for pollination (Vogel, 1961; Masinde, 2004; Ollerton, Masinde, Meve & Whittington, unpublished data). Pitfall flowers of the *Ceropegia* type also occur in *Riocreuxia*. Apart from anatomical differences (pedicels with sclerenchymatic tissue and a parallel-veined corolla, both absent in *Ceropegia*) and gynostegial dissimilarities like a style-head of the marsdeniad type (Meve, 1998; Meve & Liede, 2004: fig. 3B), the independence of *Riocreuxia* is also corroborated by molecular data (Meve & Liede, 2004). *Riocreuxia* is now placed in the Ceropegieae subtribe Anisotominae, which is sister to Stapeliinae (Meve & Liede, 2004).

Vegetative morphology. *Ceropegia* is more diverse vegetatively than florally. The growth forms encompass small geophytic, erect, or twining herbs; leafy twiners or stem-succulents (partly without leaves); or true lianas of more than 10 m height. Annuals are absent. The root system can be fibrous (Fig. 1B), can consist of fleshy, thickened secondary roots that form fusiform or cylindric storage organs (Fig. 1C), or can be a tuber formed by the primary root, often together with the hypocotyl (Fig. 1D). The fleshy secondary roots appear either in dense clusters (Fig. 1C) or are scattered over the root system. Normally, fleshy secondary roots and root tubers exclude each other (Fig. 1B–D). The three basal character states of the roots and stem succulence

or non-succulence are included in Figure 3 because they are important in recognizing groups of closely related taxa. The formation of hypocotyl/root tubers is reported for 80 of the ca. 180 species. Fusiform-fleshy secondary roots are known from ca. 50 species (cf. Meve, 2002). The lack of any underground storage organ is characteristic for another ca. 50 species. The most derived, tuberous growth form is restricted to clades C and G of the seven main clades (Fig. 3). Significantly, in clade A fibrous non-tuberous roots occur in all four species of this most early-branching clade, whereas in clade F, the Asian–Canary clade, the species of the truly Asian subclade, the *C. meleagris* H. Huber–*C. monticola* W.W. Sm.–*C. longifolia* Wall. clade (clade D), are equipped with fusiform-fleshy roots only. In contrast, the fusiform-fleshy type of root is completely absent in Madagascar (clade G2, Fig. 3).

Cytology. Numerous chromosome numbers for *Ceropegia* were included in the overview of the family by Albers and Meve (2001). Additional counts for East African taxa were contributed by Masinde (2000). All published numbers can be viewed at: <<http://www.pflanzen-systematik.uni-bayreuth.de>>. Meanwhile, additional counts have increased the number of chromosomally known species of *Ceropegia* to 74 or ca. 40% of the genus (Meve, unpublished data). For all taxa investigated, the basal chromosome number is $x = 11$. Diploids with $2n = 22$ dominate by far. Only a few taxa are characterized by a tetraploid genome of $2n = 44$ chromosomes. These are the leafy East African *C. linearis* subsp. *woodii*, *C. inornata* P. R. O. Bally ex Masinde, and *C. cufodontii* Chiov. (Meve, unpublished data); the Madagascan representatives *C. ampliata* E. Mey. and *C. racemosa* N. E. Br.; and the stem-succulent Indian species *C. juncea* Roxb. The chromosome numbers of the taxa investigated molecularly are plotted on the cladogram (Fig. 3). The majority of species have medium-sized chromosomes around the average length found for the whole tribe, which is $1.01 \mu\text{m}/\text{chromosome}$ (Albers & Meve, 2001). However, the average chromosome sizes in *Ceropegia* vary considerably between $0.81 \mu\text{m}$ and $1.58 \mu\text{m}$ (Meve, unpublished data). The largest chromosomes are found in leafy *ceropegias* with fibrous roots (e.g., *C. sankuruensis* Schltr. and *C. cumingiana* Decne., with around $1.40 \mu\text{m}$ average length) except for the stem-succulent Canary Islands species, *C. dichotoma* Haw., where the chromosomes measure only $0.87 \mu\text{m}$ on average.

DNA ANALYSIS

The cpDNA data set. The cpDNA alignment comprises 69 taxa and a total of 1973 characters

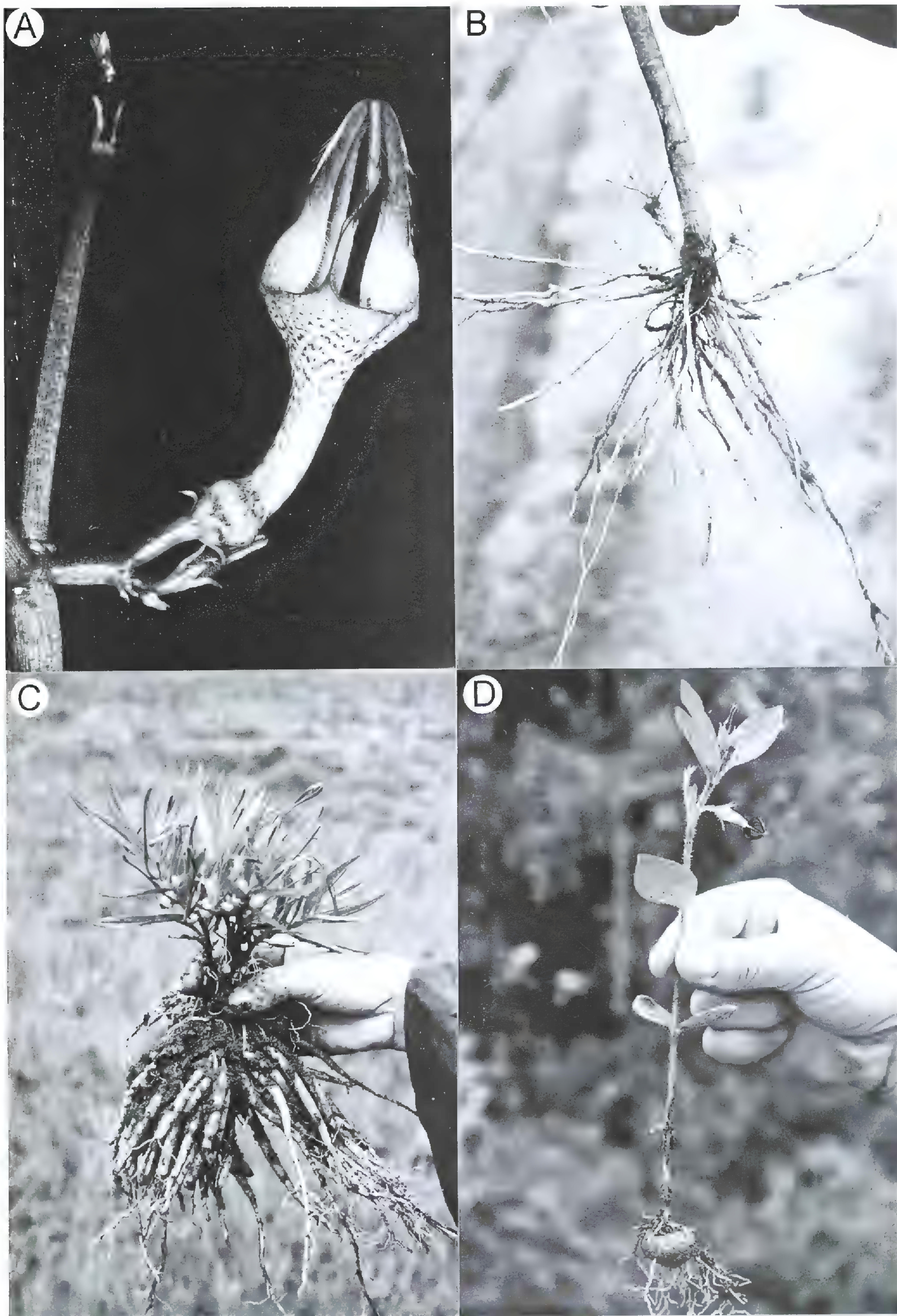


Figure 1. *Ceropegia*. —A. Flowering stem of *C. juncea*. — B. Stem base of *C. lugardiae* showing the fibrous roots. — C. Whole plant of *C. gilgiana* with cluster of swollen, fusiform roots. —D. Whole plant of *C. abyssinica* showing the root tuber. A: Řiřánek & Hanáček 92; B: Specks 1042; C: Specks 1039; D: Specks 1039. Photo: A by U. Meve; B–D by E. Specks.

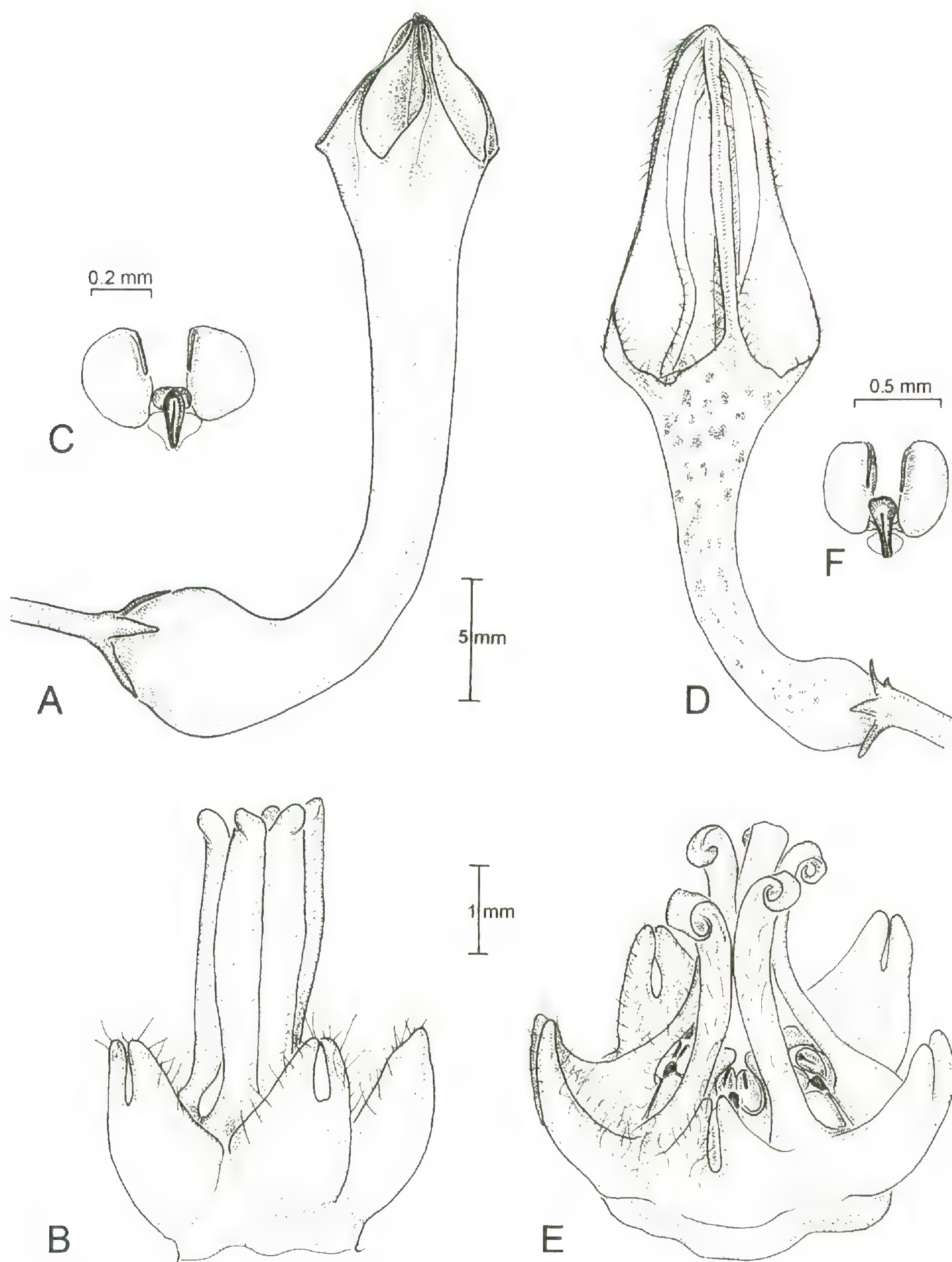


Figure 2. A–C. *Ceropegia aristolochioides* subsp. *deflersiana*. —A. Flower. —B. Corona. —C. Pollinarium. D–F. *Ceropegia juncea*. —D. Flower. —E. Corona. —F. Pollinarium. A–C: Mangelsdorff Y11 (UBT); D: ex hort. P. Shirley (UBT). E, F: Řičanek & Hanáček 92 (UBT). Drawn by U. Meve.

(1013 sequence characters in the *trnT-L* spacer [primers a and b], 551 sequence characters in the *trnL*-intron [primers c and d], and 409 sequence characters in the *trnL-F* spacer [primers e and f]); a total of 26 data cells are unknown. This alignment, as well as that for ITS, are available from the authors or can be viewed at <<http://www.pflanzensystematik.uni-bayreuth.de>> or in TreeBASE (study accession

number = S1710, matrix accession numbers = M3095 and M3096; Sanderson et al., 1994). Parsimony analysis of the cpDNA sequence characters alone (112 parsimony informative characters) resulted in more than 79,500 most parsimonious trees of 184 steps with consistency index (CI) of 0.72 (excluding uninformative characters) and retention index (RI) of 0.92.

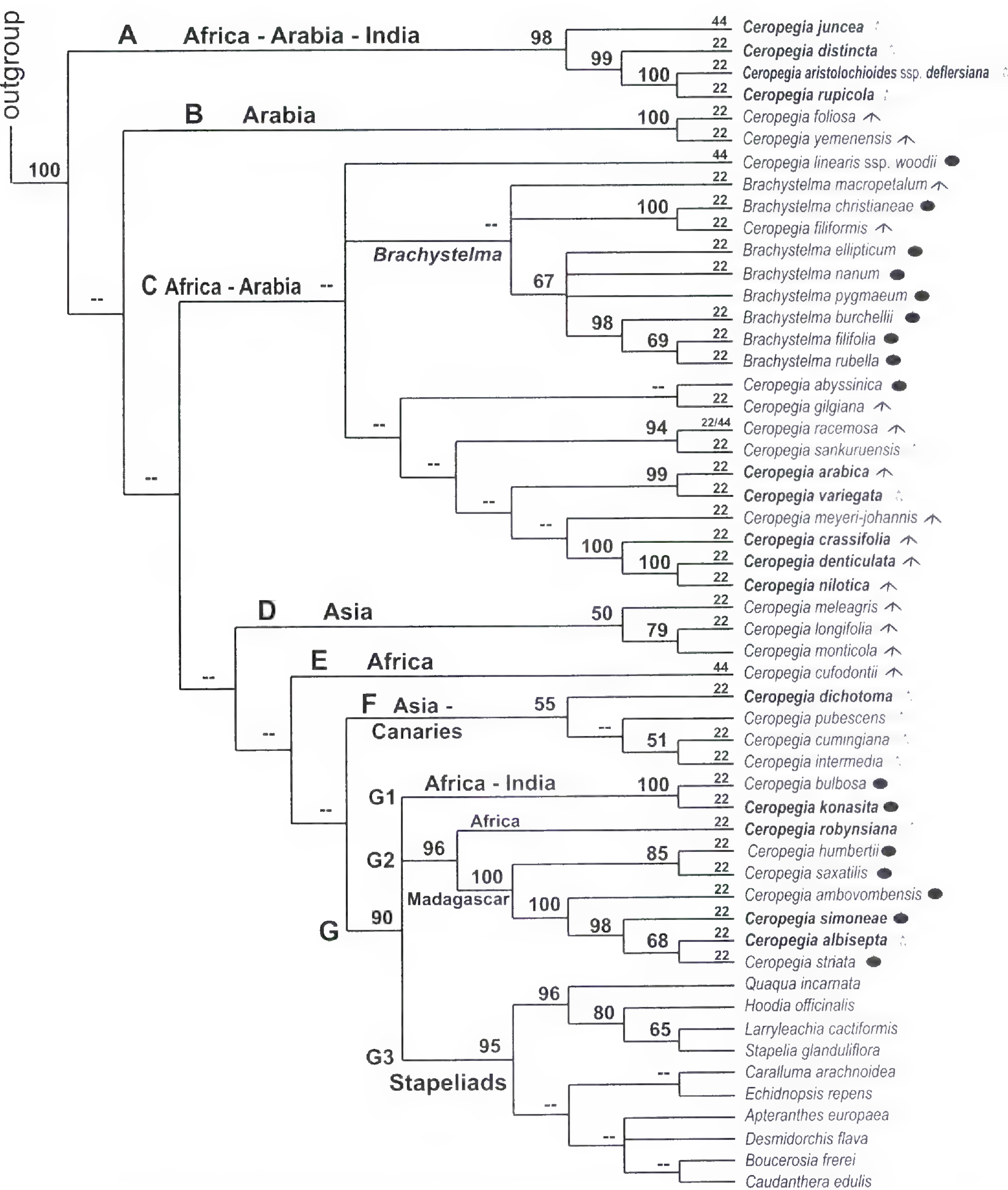


Figure 3. Strict consensus tree of 234 most parsimonious trees derived from cladistic analysis of combined ITS and *trnT-L* and *trnL-F* spacers, and the respective indels coded as binary characters (l = 1118 steps, CI = 0.5519 [excluding uninformative characters], RI = 0.8127, rescaled consistency index [RC] = 0.4458; missing data [for ITS] have been coded with “nn”). Numbers indicate bootstrap percentages; – indicates bootstrap percentage < 50%; numbers on the end branches indicate the 2*n* chromosome number of the taxon where available; stem-succulent *Ceropegia* taxa are printed in **bold**; △ = roots fibrous; ⤴ = roots fleshy-fusiform; ● = roots tuberous.

In previous analyses (Meve & Liede, 2002a, 2004) and the one presented here, the *Ceropegieae* are monophyletic and form a strongly supported clade (100% bootstrap support), as does the terminal subtribe *Stapeliinae*. Within the latter, resolution in the cpDNA analysis alone is rather low (not shown, available from authors on request). Together with 12 mostly Asian *Ceropegia* species, the stapeliads remain unresolved. Most conspicuous is the subclade formed by the endemic Madagascan *Ceropegia* taxa plus *C. robynsiana* Werderm., and a clade in which all investigated *Brachystelma* species and 12 Afro-

Arabian *Ceropegia* species are combined. However, all these clades retrieved are without statistical support or nearly so.

The ITS data set. The alignment for ITS comprises 65 taxa and a total of 713 sequence characters. Three sequences could not be generated, one was not aligned (see Materials and Methods), and seven data cells are unknown. Parsimony analysis of ITS data alone, excluding the four missing sequences (299 parsimony informative characters), resulted in more than 65,400 trees of 914 steps (not shown). CI (excluding uninformative characters) is 0.53, and RI is 0.79.

Analysis of the ITS data set (not shown, available from authors on request) results in a better-resolved tree with regard to the subclades. The whole *Ceropegia* complex remains unresolved. The stapeliads switch to a subclade with 92% bootstrap support. *Brachystelma* forms a moderately supported subclade (75% BP) within a large basal polytomy, which includes *C. filiformis* (Burch.) Schltr. The endemic Madagascan taxa, again, form a monophyletic group, now supported by 100% BP. There are several cases where sister species relationships are now supported by 100% BP (as is the same in the combined analysis, Fig. 3): *B. christianeae* Peckover and *C. filiformis*; *C. foliosa* Bruyns and *C. yemenensis* Meve & Mangelsdorff; *C. crassifolia*, *C. denticulata* K. Schum. ex Engl., and *C. nilotica* Kotschy; *C. rupicola* Deflers and *C. aristolochioides* Decne.; and *C. bulbosa* Roxb. and *C. konasita* Masinde.

The combined cpDNA and nrDNA data set. The partition homogeneity test (Cunningham, 1997) suggested that combining the data sets would generally improve phylogenetic accuracy ($P = 0.02$). Parsimony analysis of ITS combined with the *trnT-L* and *trnL-F* spacer regions (409 parsimony informative characters) resulted in 234 trees of 1118 steps, with CI (excluding uninformative characters) of 0.55 and RI of 0.81 (Fig. 3). In this analysis, the species with missing ITS sequences have been eliminated.

Of all data sets analyzed, the combined data set (Fig. 3) shows the highest resolution and, in general, better support for clades retrieved in the individual cpDNA and ITS analysis. The statistical support of the subclade showing the monophyly and the sister relationship of the Madagascan taxa to the East African *Ceropegia robynsiana* is strong (96% BP). The purely Madagascan subclade (100% BP) falls into two subclades. The first is a moderately supported subclade (85% BP) containing the leafy and tuberous *C. humbertii* H. Huber and *C. saxatilis* Jum. & H. Perrier; the other is a strongly supported subclade

(100% BP) comprising a diverse blend of taxa representing all main growth forms described for Madagascar endemics. The strongly supported clade A (98% BP) comprising the non-tuberous *C. juncea*, *C. aristolochioides* subsp. *deflersiana* Bruyns, *C. distincta* N. E. Br., and *C. rupicola* now appears at the base of the cladogram as sister to the rest of Stapeliinae. There is no statistical support for most of the remaining main clades. The large clade C, shared by 12 *Ceropegia* and all *Brachystelma* species investigated, is nested in the middle of the ingroup, making *Ceropegia* without *Brachystelma* paraphyletic. In the terminal clade G (90% BP), the well-supported subclades G1 (*C. bulbosa*–*C. konasita*, 100% BP), G2 (*C. robynsiana* plus the Madagascan group, 96% BP), and G3 (stapeliads, 95% BP) form a terminal polytomy. Thus, *Ceropegia* without the stapeliads is paraphyletic in this second case. However, all three subclades of clade G represent strongly supported monophyletic groups (Fig. 3). *Ceropegia* thus forms a grade of seven clades (A–G) pointing to complex infrageneric relationships. *Ceropegia* species mostly cluster according to geographical distribution; in some cases, the growth form serves as a good marker for close relationship (Fig. 3: clades A, D, F). Unexpectedly, the Canary Island species, *C. dichotoma*, shares a clade with three taxa from India and Australasia (clade F), although statistical support is low (55% BP). *Ceropegia juncea*, restricted to India where it is morphologically isolated by its succulent stems and reduced leaves, shares clade A with East African–Arabian taxa (85% BP; Fig. 3).

DISCUSSION

Chromosome numbers show little variation at the genus level in *Ceropegia*. However, at species level they are significant. The occurrence of diploid specimens of *C. ampliata* and *C. racemosa* in Africa and tetraploid specimens in Madagascar has been interpreted as proof of long-distance dispersal from Africa to Madagascar, because polyploidy is a unidirectional event (Meve & Liede, 2002b). The other few known polyploids seem to occur randomly scattered over South Africa, East Africa, and India (cf. Fig. 3). Also noteworthy is the trend toward larger chromosomes in the non-tuberous species; this has been demonstrated in the studies of Albers and Meve (2001) in Periplocoideae, Secamonoideae, and Asclepiadoideae, which show a general trend from larger chromosomes in basal taxa to smaller chromosomes in the most advanced tribe, Asclepiadeae. *Ceropegia dichotoma*, endemic to the Canary Islands, has unusually small chromosomes within the genus and could then be interpreted as possibly the most

advanced species sampled in this study. Bruyns (1986) regarded some floral characters of this species, such as the poorly or uninflated corolla tube or the small gynostegium, as primitive. This interpretation, however, is not supported in our phylogeny (clade F, Fig. 3). Interestingly, *C. dichotoma* is in a weakly supported clade (55% BP) with the Asian, non-succulent, fibrous-rooted taxa *C. pubescens* Wall., *C. intermedia* Wight, and *C. cumingiana*. *Ceropegia dichotoma*, as well as its sister species *C. fusca* Bolle, therefore might have reached the Canary Islands more recently, where the stem-succulent growth then evolved in response to the special semi-arid and volcanic environment. This growth form, the lack of leaf petioles and peduncles, the small chromosomes, and the floral peculiarities mark it as a highly specialized species that evolved in island isolation. This combination of characters is not known otherwise in the genus. Elsewhere, *Ceropegia* has shown considerable radiative potential (e.g., in Madagascar), whereas in the Canary Islands it is restricted to *C. dichotoma* (including two subspecies) and *C. fusca*, all of which point toward a rather recent arrival of *Ceropegia* on the Canaries.

Molecular phylogeny and vegetative morphology are often linked to geography (cf. Fig. 3). A morphological exception is the unexpected sister relationship of *Ceropegia filiformis* and *Brachystelma christianeae*, since *C. filiformis* has fusiform-fleshy roots and typical *Ceropegia* pitfall flowers, whereas *B. christianeae* has a single tuber and flat, radiate flowers. However, *B. christianeae* does not have the pubescent pedicels and abaxial corolla typical for *Brachystelma*; conversely *C. filiformis* has a swollen style-head that projects above the anthers, which is unknown in *Ceropegia* but occurs occasionally in *Brachystelma* (Bruyns, 1995). Thus, neither species fits within the general concepts of their respective genera, but, in contrast, they also do not share morphological features indicating close relationship apart from their very small habit and wiry stems. Nevertheless, their sister relationship is strongly supported here (100% BP, Fig. 3) and is also supported by shared indels, which cannot be easily ignored taxonomically. Morphological transitions between *Ceropegia* and *Brachystelma* are not restricted to this case, however. There are other borderline cases, such as *B. mafekingense* N. E. Br. and *B. gymnopodium* (Schltr.) Bruyns, which have been moved between *Ceropegia* and *Brachystelma* in the past (cf. also Bruyns, 1995). In all these cases, introgression via interspecific and intergeneric hybridization events are most likely responsible for these patterns. Because small flies (see Results: Flower Morphology, above) are involved in the pollination of

both *Brachystelma* and *Ceropegia* and because many species of each genus share similar floral attractants (Meve & Liede, 1994b), the most important prerequisites for cross-pollination are already in place.

Taxonomically, inclusion of *Brachystelma* (ca. 120 species) in *Ceropegia* (180+ species) would solve part of the problem; however, the morphological concept of *Ceropegia* (see below) would be demolished, and the many name changes would be unpleasant. Nevertheless, this option should be kept in mind. Before such a step is undertaken, however, additional *Brachystelma* species, especially from Asia, should be included in sequence analysis.

Non-tuberous species occur in all the main clades retrieved (Fig. 3). As far as resolution allows, these taxa then typically appear in less-derived positions. This is true for the terminal polytomy of clade G (with *Ceropegia robynsiana*); the intermediate polytomy of clade C, which includes *Brachystelma* (with *C. sankuruensis*); the subclade F as sister to the terminal polytomy (with *C. dichotoma*); and the subclade A as sister to all Stapeliinae with all species (*C. juncea*, *C. distincta*, *C. aristolochioides*, and *C. rupicola*). Fibrous roots, always present in the stem-succulent stapeliads, are recognized as a symplesiomorphy for the Stapeliinae and also for the tribe Ceropegieae, because the basal three subtribes (Heterostemminae, Anisotominae, and Leptadeniinae; Meve & Liede, 2004) also lack root succulence, except for slightly swollen secondary roots in *Sisyranthus* (Anisotominae). This sounds trivial, but in the most basal tribe of Asclepiadoideae, the Fockeeae (Verhoeven et al., 2003), root tubers are the rule. The minority of *Ceropegia* species have such plesiomorphic fibrous roots (see above; Fig. 3). Concerning stems and leaves, non-succulence, again, must be regarded as plesiomorphic because all other and basal representatives (the subtribes Heterostemminae, Anisotominae, and Leptadeniinae) have “normal,” sometimes slightly woody stems and mesophyllous, sometimes slightly xerophytic leaves. Indian species such as *C. intermedia* or *C. pubescens*, as well as the Australasian *C. cumingiana*, also share these morphologically less-specialized features, although they are found in an intermediate position in our phylogeny (clade F). Although flower morphological parallelisms (homologies) in response to pollinator pressure should always be taken into consideration in the asclepiads (e.g., Meve & Liede, 1999, 2002a), the similarities in the morphology of the gynostegia, coronas, and pollinaria of *C. juncea* and, for example, *C. aristolochioides* subsp. *deflersiana* (Fig. 2) are striking. In particular, the deltoid corpuscle projections and pollinia possessing rather triangular and more or less membranous margins (germination crests) are mor-

phologically significant for this group (clade A, Fig. 3). Taxa such as *C. somalensis* Chiov., *C. yorubana* Schltr., and *C. zambesiaca* Masinde & Meve should be included in this group based on morphological grounds. These morphological characters are useful systematic markers here, especially since they are congruent with the results of molecular analysis. The situation is similar to that found in *C. dichotoma* and, for example, *C. pubescens* (clade F, Fig. 3). Although these two taxa are vegetatively quite different, the peculiar structure of their gynostegium and corona, in which the interstaminal coronas are almost completely reduced and fused to the backs of the staminal corona (cf. figs. in Bruyns, 1986), is very similar. These corona peculiarities also appear in other Asian taxa such as *C. hookeri* C. B. Clarke ex Hook. f. However, other members in this non-tuberous group of taxa (clade A) do not share this type of corona, so that interpretation as a homoplasy cannot be excluded.

SUCCESS IN GAINING A MOLECULAR PHYLOGENY AND ITS TRANSLATION INTO TAXONOMY

Inclusion of more species into the molecular phylogeny and, perhaps, the use of an additional molecular marker might improve the resolution and the statistical support of the *Ceropegia* cladogram(s). However, there is reasonable doubt that the result would lead to a phylogeny more easily transposed into taxonomy than the one presented here. Quite possibly, the number of clades would increase further. As could be expected when starting an analysis of a large and widely distributed genus such as *Ceropegia*, the cladograms constructed from the molecular data do not answer all the questions. Worse yet, numerous questions arise where there were none before. *Ceropegia* species appear in seven different clades; the six most early branching clades form a grade and include *Brachystelma* (Fig. 3, clade C), while the remaining clades are part of a terminal polytomy that falls into three well-supported subclades and also includes the stapeliad clade. The most early branching clade A, and only this clade, includes representatives from all main distribution areas (Africa, Arabia, Asia) except for Madagascar. Thus, an area of origin for *Ceropegia* can hardly be determined. However, East African/Arabian taxa dominate in clade A, which is followed, again, by two clades containing only African/Arabian taxa, so that the available data could be interpreted as support for a northeast African center of origin. This area has also been determined to be the primary evolutionary center for the stapeliads, in particular, *Caralluma* s. str. (Meve, 1997; Meve & Liede, 2002a). Restricted to just two clades, D and F, several Asian taxa appear, in contrast to the isolated

Ceropegia juncea in clade A; however, there is no substantial statistical support for these clades. This grouping might indicate that the recent Asian taxa have developed more or less independently from the rest of the genus for a longer time, and that the origin of the genus cannot be located in Asia. These nearly exclusively Asian clades, nevertheless, include one taxon from the western distribution area, the Canary Islands endemic *C. dichotoma*. This indicates that the Canary Islands taxa, surprisingly, have no close African relative left when long-distance dispersal from West African progenitors is supposed, although accessory species in the analysis might change this impression. The endemic Madagascan taxa are grouped together on subclade G2 (Fig. 3) and are sister to *C. robynsiana*. Madagascar, therefore, has been obviously invaded just once (excluding *C. ampliata* and *C. racemosa*, see below) and comparatively late by a *Ceropegia* related to East African species such as *C. robynsiana*, which then served as progenitor of today's phenetically rather diverse but genetically closely interrelated Madagascan stock. A classification restricting section *Dimorpha* to stem-succulent Madagascan taxa alone (Meve & Liede, 1994a), therefore, should be rejected. Instead, section *Dimorpha* should cover all *Ceropegia* species endemic to Madagascar, including *C. robynsiana*. However, this section then would seem to have no morphological synapomorphy left. The situation in *Ceropegia* on Madagascar, with a late arrival by rather derived taxa followed by considerable diversification, is reminiscent of the situation in the highly diverse and variable genus *Impatiens* L. (Balsaminaceae), where the most basal taxa are found in South and Southeast Asia (Yuan et al., 2004). The two nonendemic *Ceropegia* species also found in Madagascar, *C. ampliata* and *C. racemosa*, have been identified as not being closely related to the Madagascan stock (Huber, 1957; Meve & Liede, 1994a). Both are tetraploid in Madagascar, diploid in Africa (Meve & Liede, 2002b), and nested within their African relatives of clade C (molecularly tested for *C. racemosa* only). Thus, all three of these data sets strongly suggest that both *Ceropegia* species reached Madagascar rather recently by means of long-distance dispersal (Meve & Liede, 2002b).

Finally, the well-supported position of the sisters, *Ceropegia bulbosa* from India and *C. konasita* from Africa, on the terminal polytomy (clade G) remains unexplained, but suggests another colonization of Asia by African stock. Infrageneric patterns are too reticulate morphologically to allow revision at the sectional level. Single groups of taxa (e.g., clades A, F, and subclade G2; Fig. 3) represent good candidates for sections should sectional classification be appropriate later when more data become available.

Brachystelma (ca. 120 species) and the stapeliads (ca. 400 species) are nested within different lineages of *Ceropegia*, therefore rendering it paraphyletic. Transferring the cladification presented here into classification would mean either reducing the subtribe Stapeliinae to one single genus or splitting *Ceropegia* into seven or eight genera (with *Brachystelma* included in a genus representing clade C). Neither the first nor the second solution is a desirable option. Either way, none of these newly created genera could be characterized by a specific set of morphological character states, and almost none could be keyed out morphologically. Considering the rather convincing current taxonomy, as well as the many phenetic differences between and, most important, within the groups involved, such translation of cladistics into classification is rejected here. As Brummitt (1996) and Grant (2003) pointed out, the paraphyly concept belongs to cladistics and not to taxonomy. This statement is especially pertinent when the cladistic results are based on the analysis of few non-genomic markers and where they are highly incongruent with the morphological characters commonly used in taxonomy. Diverse molecular studies in Asclepiadoideae have provided many new insights into possible phylogenies and relationships, and paraphyletic groups have been identified in several cladistic analyses as well. Sometimes these paraphyla contradicted the then-current taxonomy at first glance, but reconsideration of morphological data, for example, revealed the traditional view to be one-sided. For example, the former genera *Sarcostemma* R. Br., *Karimbolea* Desc., *Folotsia* Costantin & Bois, and *Platykeleba* N. E. Br. were taxonomically separated from similarly leafless and stem-succulent *Cynanchum* L. for decades because of their aberrant corona structure. Molecular analysis (Liede & Kunze, 2002; Liede & Täuber, 2002), however, has shown that, without exception, all of these stem-succulent taxa form a well-supported, monophyletic subgroup within *Cynanchum*, a plausible result that is corroborated by morphological (stems and leaves), anatomical (Liede & Kunze, 2002), and also biogeographical data, since Meve and Liede (2002b) have shown that this group originates in Madagascar. The case presented in the present paper, however, does not offer such a “smooth” solution, possibly because this study deals with a very fast-evolving genus (cf. Klak et al., 2004), in which hybridization events result in a reticulate molecular phylogeny (cf. Sosef, 1997). As long as molecular and “classical” data remain incongruent to the degree exhibited in *Ceropegia*, paraphyly must be acceptable for taxonomists aiming to produce a classification that allows recognition of the organisms. Recently, in an open letter to the editor of the journal *Taxon* signed by

over a hundred taxonomists, the appeal has emphatically been made that “Paraphyly should be accepted” (Nordal & Stedje, 2005). *Ceropegia*, as has been shown here, represents a group of closely related and interrelated taxa, but its recognition as a monophyletic taxon failed. The taxa are nevertheless held together by a wide array of specific morphological characteristics. In this special situation, we feel it is most prudent to uphold the current taxonomy.

Literature Cited

- Albers, F. & U. Meve. 2001. A karyological survey of Asclepiadoideae, Periplocoideae and Secamonoideae, and evolutionary considerations in Apocynaceae s.l. *Ann. Missouri Bot. Gard.* 88: 624–656.
- Ansari, M. Y. 1984. Pp. 1–35 in *Asclepiadaceae: Genus—Ceropegia*. Fascicles of Flora of India, Vol. 16. Botanical Survey of India, Howrah.
- Brummitt, R. K. 1996. In defense of paraphyletic taxa. Pp. 22–27 in L. J. G. van der Maesen, X. M. van der Burgt & J. M. van Medenbach de Roy (editors), *The Biodiversity of African Plants. Proc. XIV AETFAT Congress, 22–27 August 1994, Wageningen*. Kluwer Academic Publishers, Dordrecht.
- . 2002. How to chop up a tree. *Taxon* 51: 31–41.
- Bruyns, P. V. 1985. Notes on *Ceropegias* of the Cape Province. *Bradleya* 3: 1–47.
- . 1986. The genus *Ceropegia* on the Canary Islands (Asclepiadaceae-Ceropédieae). A morphological and taxonomic account. *Beitr. Biol. Pflanzen* 60: 427–458.
- . 1995. New records and new species of Asclepiadaceae. *Bothalia* 25: 155–172.
- Cunningham, C. W. 1997. Can three incongruence tests predict when data should be combined? *Molec. Biol. Evol.* 14: 733–740.
- Doyle, J. J. & J. L. Doyle. 1987. A rapid DNA isolation procedure for small quantities of fresh leaf tissue. *Phytochem. Bull.* 19: 11–15.
- Dyer, R. A. 1980. Asclepiadaceae (*Brachystelma*, *Ceropegia*, *Riocreuxia*). Pp. 1–90 in O. Leistner (editor), *Flora of Southern Africa*, Vol. 27(4). Government Printer, Pretoria.
- . 1983. *Ceropegia*, *Brachystelma* and *Riocreuxia* in Southern Africa, 1st ed. Balkema, Rotterdam.
- Felsenstein, J. 1985. Confidence limits on phylogenies: An approach using the bootstrap. *Evolution* 39: 783–791.
- Gilbert, M. G. 2003. *Ceropegia* L. (1753). Pp. 158–169 in I. Hedberg, S. Edwards & S. Nemomissa (editors), *Flora of Ethiopia and Eritrea, Apiaceae to Dipsacaceae*, Vol. 4(1). The National Herbarium, Addis Ababa.
- Grant, V. 2003. Incongruence between cladistic and taxonomic systems. *Amer. J. Bot.* 90: 1263–1270.
- Huber, H. 1957. Revision der Gattung *Ceropegia*. *Mem. Soc. Brot.* 12: 1–203.
- Klak, C., G. Reeves & T. A. Hedderson. 2004. Unmatched tempo of evolution in southern African semi-desert ice plants. *Nature* 427: 63–65.
- Liede, S. & H. Kunze. 2002. *Cynanchum* and the *Cynanchinae* (Apocynaceae-Asclepiadoideae): A molecular, anatomical and latex triterpenoid study. *Organisms Diversity Evol.* 2: 39–269.
- & A. Täuber. 2002. Circumscription of the genus *Cynanchum* (Apocynaceae-Asclepiadoideae). *Syst. Bot.* 27: 789–801.

- Masinde, P. S. 2000. Systematic Studies in the Genus *Ceropegia* L. (Asclepiadaceae-Stapelieae) in East Africa. Dissertation, Westf. Wilhelms-Univ. Münster, Münster, Germany.
- . 2004. Trap-flower fly pollination in East African *Ceropegia* L. (Apocynaceae). *Int. J. Trop. Insect Sci.* 24: 55–72.
- Meve, U. 1997. The genus *Duvalia* (Stapelieae). Springer, Vienna.
- . 1998. *Emplectanthus* N. E. Br.: A close relative of *Riocreuxia* Deene. in the Asclepiadaceae-Stapelieae. *Bot. Jahrb. Syst.* 120: 123–130.
- . 2002. *Ceropegia*. Pp. 63–107 in F. Albers & U. Meve (editors), *Illustrated Handbook of Succulent Plants: Asclepiadaceae*. Springer, Heidelberg.
- & S. Liede. 1994a. A conspectus of *Ceropegia* L. (Asclepiadaceae) in Madagascar, and the establishment of *C. sect. Dimorpha*. *Phyton (Horn)* 34: 131–141.
- & ———. 1994b. Floral biology and pollination in stapeliads: New results and a literature review. *Pl. Syst. Evol.* 192: 99–116.
- & ———. 1999. Floral morphological convergences, a common source of taxonomic misplacements in Asclepiadoideae. P. 709 (Poster 2495) in *Abstracts, XVI International Botanical Congress, St. Louis*.
- & ———. 2001. Inclusion of *Tenaris* and *Macropetalum* in *Brachystelma* (Apocynaceae-Asclepiadoideae-Ceropegieae) inferred from non-coding nuclear and chloroplast DNA sequences. *Pl. Syst. Evol.* 228: 89–105.
- & ———. 2002a. A molecular phylogeny and generic rearrangement of the stapelioid Ceropegieae (Apocynaceae-Asclepiadoideae). *Pl. Syst. Evol.* 234: 171–209.
- & ———. 2002b. Floristic exchange between mainland Africa and Madagascar: A case study of Apocynaceae-Asclepiadoideae. *J. Biogeogr.* 29: 865–873.
- & ———. 2004. Subtribal division of Ceropegieae (Apocynaceae-Asclepiadoideae). *Taxon* 53: 61–72.
- & R. D. Mangelsdorff. 2001. A new *Ceropegia* species from Yemen, and reconsideration of the status of *C. arabica*, *C. barbiger* and *C. powysii* (Apocynaceae: Asclepiadoideae-Ceropegieae). *Bot. J. Linn. Soc.* 137: 99–105.
- , P. S. Masinde, U. Sentner & S. Liede. 2001. RAPD analysis and taxonomic reconsideration of the *Ceropegia aristolochioides* complex (Apocynaceae-Ceropegieae). *Pl. Biol. (Stuttgart)* 3: 622–628.
- Nordal, I. & B. Stedje. 2005. Paraphyletic taxa should be accepted. *Taxon* 53: 5–6.
- Sanderson, M. J., M. J. Donoghue, W. Piel & T. Eriksson. 1994. TreeBASE: A prototype database of phylogenetic analyses and an interactive tool for browsing the phylogeny of life. *Amer. J. Bot.* 81: 183.
- Schumann, K. 1895. Asclepiadaceae. Pp. 189–305 in A. Engler & K. Prantl (editors), *Die natürlichen Pflanzenfamilien*. Engelmann, Leipzig.
- Snow, R. 1963. Alcoholic hydrochloric acid-carmines as stain for chromosomes in squash preparations. *Stain Technol.* 38: 9–13.
- Sosef, M. S. M. 1997. Hierarchical models, reticulate evolution and the inevitability of paraphyletic supraspecific taxa. *Taxon* 46: 75–85.
- Swofford, D. L. 1998. *PAUP*: Phylogenetic analysis using parsimony (*and other methods)*, 4th ed. Sinauer Associates, Sunderland, Massachusetts.
- Taberlet, P., L. Gielly, G. Pautou & J. Bouvet. 1991. Universal primers for amplification of three non-coding regions of chloroplast DNA. *Pl. Molec. Biol.* 17: 1105–1109.
- Tjio, J. H. & A. Levan. 1950. The use of oxychinoline in chromosome analysis. *Anales Estac. Exp. Aula Dei* 2: 21–64.
- Verhoeven, R. L., S. Liede & M. E. Endress. 2003. The tribal position of *Fockea* and *Cibirhiza* (Apocynaceae: Asclepiadoideae): Evidence from pollinium structure and cpDNA sequence data. *Grana* 42: 70–81.
- Vogel, S. 1961. Die Bestäubung der Kesselfallenblüten von *Ceropegia*. *Beitr. Biol. Pflanzen* 36: 159–237.
- . 1962. Duftdrüsen im Dienste der Bestäubung. *Akad. Wiss. Mainz, Abh. Math.-Naturwiss. Kl.* 13: 601–763.
- Yuan, Y.-M., Y. Song, K. Geuten, E. Rahelivolonona, S. Wohlhauser, E. Fischer, E. Smets & P. Küpfer. 2004. Phylogeny and biogeography of Balsaminaceae inferred from ITS sequences. *Taxon* 53: 391–403.